

Stream macroinvertebrate community responses to fire: are they the same in different fire-prone biogeographic regions?

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Abstract: Droughts, fires, and floods are natural disturbances influencing aquatic ecosystems. If drought is accompanied by fires, and if fires are closely followed by floods, teasing apart their distinctive and potentially interactive responses can be difficult. We compared the responses of macroinvertebrate communities to fire via comparisons of streams in burned and unburned catchments in 3 fire-prone biomes that differ biogeographically and climatically (northwestern Mediterranean, southeastern Australia, and northwestern intermountain USA). The responses of macroinvertebrate communities in streams in burned catchments were similar in all biogeographic regions, but the magnitude of these responses varied. Fire combined with high seasonal stream flows, flooding, or drought was associated with reduced measures of taxonomic richness and increased abundance, especially of *r*-strategist taxa. Differences between sites in burned and unburned catchments were consistently stronger in southeastern Australia than in northwestern intermountain USA and northwestern Mediterranean regions. Our observations suggest that the timing and magnitude of postfire flows (snowmelt, seasonal high flows) may substantially alter the recolonization process and override fire effects, and that drought may play a strong role in limiting the resilience and resistance of macroinvertebrate communities in streams in catchments that have experienced wildfire.

Key words: disturbance, drought, high seasonal stream flows, beta diversity, resilience, *r*-strategist taxa

A general consensus exists that natural disturbances play a significant role in determining the distribution, abundance, and structure of stream macroinvertebrate communities (Resh et al. 1988, Fisher and Grimm 1991, Poff 1992, Downes et al. 1998, Lake 2000, Lytle 2008). After a disturbance, recolonization depends on the availability of suitable substrate, refuge, and food (Mackay 1992). Furthermore, the hierarchical and dendritic structure of river networks may impose dispersal constraints on lotic macroinvertebrate communities, which are likely to be structured by a combination of environmental factors and dispersal ability that together may impose particularly strong effects on β diversity (Clarke et al. 2010).

Droughts, fires, and floods can be extreme disturbances. They can be characterized by attributes including

severity, frequency, magnitude, predictability, duration, and spatial extent (Lake 2000, Dodds 2002). Fires and floods are considered pulse disturbances, whereas droughts are ramp disturbances that increase steadily in strength and spatial extent over time (Lake 2000). The combination of the disturbance and the ecological response constitutes a perturbation (Bender et al. 1984). The ecological response to disturbance incorporates resistance (the capacity to survive the disturbance) and resilience (the capacity to recover from disturbance) (Glasby and Underwood 1996, Lake 2000). The short-term consequences of disturbance to assemblages of stream biota are frequently negative, but the longer-term and larger-scale consequences for species diversity and abundance can be variable (Lepori and Hjerdt 2006).

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Wildfires may influence stream macroinvertebrates by many means. Fire may result in the loss of riparian vegetation, which could increase stream temperatures and change the type of available food for macroinvertebrates because of a reduction in allochthonous resources, whereas elevated light and nutrient inputs may increase autochthonous production (e.g., Minshall et al. 1997, Betts and Jones 2009, Rugenski and Minshall 2014). The strength of these responses is likely to depend on fire severity, proximity, timing, and postfire hydrologic conditions (Minshall et al. 2001a, Romme et al. 2011). Burned catchments may have more exposed soil and unstable slopes, increasing the likelihood of erosion, especially during heavy rainfall. Erosion may lead to increased transport and deposition of sediment, ash, and charcoal in stream channels and alter channel morphology, thereby affecting many stream biota negatively (Gresswell 1999, Minshall 2003). These initial indirect effects of fire on aquatic macroinvertebrates may be severe, but recovery can be relatively rapid with the macroinvertebrate community returning to its prefire condition in 1 to 2 y in some cases (Roby and Azuma 1995, Minshall et al. 2001b). However, certain taxa, such as mollusks, take substantially longer to recover (Vila-Escalé 2008). After severe wildfires, community composition may shift toward a disturbance-adapted community, characterized by taxa with short generation times, high fecundity, and high dispersal rates, so called *r*-strategists, such as Chironomidae, Baetidae, and Simuliidae (Mihuc and Minshall 1995, Vieira et al. 2004, Mellon et al. 2008, Vila-Escalé 2008, Malison and Baxter 2010). The recovery of stream macroinvertebrates after fire also may be linked to the rate at which riparian vegetation and geomorphological conditions recover (Minshall et al. 2001a, c, Verkaik et al. 2013a), but whether they will return to their prefire state under changing climate conditions is uncertain (Davis et al. 2013a).

Predictions regarding the effect of climate change on running waters vary among regions, but alterations in hydrology and thermal regimes are expected in most rivers (Malmqvist and Rundle 2002) and, in many parts of the world, incorporating the effects of changing fire regimes may be essential to such predictions (Davis et al. 2013a). A warmer, drier climate may modify the frequency and severity of wildfires (Krawchuk et al. 2009). Changes in land use and forest-management policies, such as wildfire suppression or prescribed burning practices, also affect vulnerability to fire (Turner et al. 2003, Lavorel et al. 2007, Moritz et al. 2014). Under these scenarios, variation in fire regimes combined with altered flow regimes may increase the difficulty of generalizing across regions regarding responses of stream macroinvertebrate communities to fire. However, regional comparisons might help to evaluate this generality.

If drought is accompanied by fires, and if fires are closely followed by floods, teasing apart the distinctive or interac-

tive responses can be difficult (Verkaik et al. 2013a, b, 2014, Rugenski and Minshall 2014). For example, differences between prefire and postfire macroinvertebrate community composition provided evidence that repeated flash floods after fire shaped community succession (Vieira et al. 2004). In intermittent streams, fire can damage dry biofilms and influence algal recolonization (Cowell et al. 2006), whereas consecutive, severe seasonal droughts after fire may reduce macroinvertebrate taxonomic richness and abundance and change the community (Verkaik et al. 2013b). On the other hand, the effects of fire on macroinvertebrate communities also may be moderated by reduced precipitation or spring runoff resulting from low snowpack levels (Rugenski and Minshall 2014).

We present the results of a study comparing the responses of macroinvertebrate communities to fire in 3 biomes that differ biogeographically and climatically (northwestern Mediterranean, southeastern Australia, and northwestern intermountain USA). We used a comparative sampling design (i.e., space-for-time substitution of burned and unburned sites) rather than a before–after design (i.e., pre- and post-fire) and did not measure macroinvertebrate resilience per se. Therefore, we use the word ‘response’ to describe any differences. Overall, we expected: 1) lower taxonomic richness of macroinvertebrate communities at sites in burned than in unburned watersheds 9 to 11 mo after fire; 2) changes in the composition of the macroinvertebrate communities, with increased dominance by more generalist *r*-strategist taxa; and 3) differences in macroinvertebrate community responses among regions controlled by postfire climate and hydrology, and, in particular, that high flows may reset recovery trajectories, whereas drought may delay recovery.

METHODS

Study sites

Macroinvertebrate data were collected in 3 study areas: 1) central Idaho (IDA) in the intermountain northwestern USA within the Payette National Forest on the South Fork of the Salmon River (lat 44°42'41"–44°54'44"N, long 115°41'04"–115°45'21"W), 2) southeastern Australia in Victoria (VIC) in the Goulburn and Ovens river catchments (lat 36°25'9"–36°33'40"S, long 145°32'55"–146°6'25"E), and 3) northeastern Spain, in the Natural Park of Sant Llorenç de Munt in Catalonia (CAT) in the headwater streams of the Besòs and Llobregat rivers (lat 46°7'2"–46°10'9"N, long 41°34'48"–42°30'59"E) (Fig. 1). Fire is a common disturbance in all 3 areas, and generally occurs during dry, hot summers and creates a mosaic of areas with different postfire vegetation. However, these 3 biogeographic regions differ in climate, vegetation, hydrology, and elevation (Table 1).

IDA has the highest elevation and a cold-temperate climate (Table 1). Most of the annual precipitation occurs as snow, resulting in peak flows during spring and early

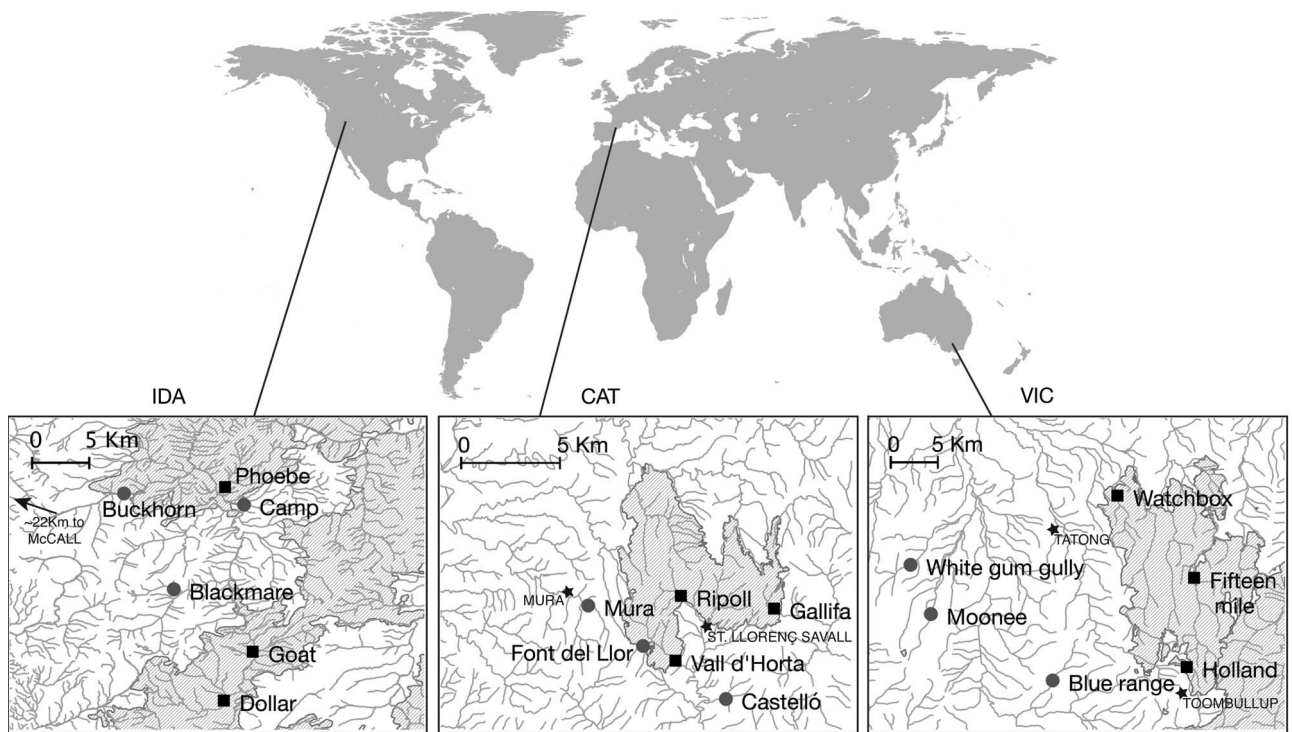


Figure 1. Locations of the streams studied in each biogeographic region (IDA = Idaho, VIC = Victoria, CAT = Catalonia) showing the closest settlements. The shaded area represents the burned area, sites in burned catchments are represented as black squares, and sites in unburned catchments are represented as gray circles.

summer (May and June) and base flow from midsummer through autumn (July–November). Study streams were in the South Fork of the Salmon River basin, where they cut through steep valleys with forested slopes (Table 1). At the time of the study, the streams ranged in channel width from 2.5 to 10.8 m and had a mean depth of 11 to 26 cm. Existing fire-history information for the study area from years 1740–1900 (using charcoal and scar studies) indicated a fire recurrence of 8 to 32 y (Heyerdahl et al. 2008). The most recent information of the fire history in the Idaho study area obtained from the National Atlas (<http://www.nationalatlas.gov/index.html>, accessed December 2009) indicated that no fires occurred in the study stream catchments from 1995 to 2000. Prefire precipitation (beginning in autumn 2006 and continuing into the spring of 2007) was ~50% of the long-term average (Western Regional Climate Center, accessed August 2014; Graham et al. 2009). As a result, in April 2007, central Idaho experienced moderately dry conditions that compounded into severe drought in July according to the Palmer Z-Index (National Climatic Data Center, accessed August 2014). Under these conditions, lightning ignited many fires including the East Zone Complex Fire, which burned >95,000 ha between end of July and mid-September 2007 (Tily 2008), encompassing the catchment area of our study.

VIC is hilly and dominated by *Eucalyptus* species (Table 1). The climate is warm-temperate, with cool, wet winters and

warm, dry summers. At the time of our study, the channel profile of the studied streams was mainly shallow with a width of 1.5 to 3.2 m and depth of 8 to 30 cm. During the period between 1970 and 2007 timely prescribed minor burns (<6.8%; see Verkaik et al. 2014) took place in 2 of the study stream catchments, but none of them experienced wildfire (Biodiversity Interactive Map of the Department of Sustainability and Environment, accessed December 2009). The fire season 2006–2007 in VIC began northeast of the region in early December and was heightened by exceptionally dry conditions (Smith 2007, Bond et al. 2008). More than 1.2 million ha of private and public land were burned, including parts of the upper catchments of the Goulburn and Ovens rivers (Smith 2007). In addition to fire, the area was affected by 13 consecutive years of below-average rainfall and a >50% reduction in runoff (Thomson et al. 2012).

CAT is predominantly hilly with wet winters and hot, dry summers (Table 1). Large floods in winter/autumn and seasonal droughts in summer produce the intermittency of these Mediterranean streams (Gasith and Resh 1999). At the time of our study, the channel profile of the studied streams varied in width from 0.3 to 4.8 m and depth from 8 to 30 cm. The area has a long history of wildfires, but most of the fires occurring between 1965 and 2003 were quickly extinguished (Santos et al. 2009). However, the 1994 fire burned 143 ha and affected 15.8% of the catchment of the Vall d'Horta stream. In August 2003, the dry

Table 1. Summary of the main characteristics of the 3 biogeographic regions where the study was conducted. Min = minimum, max = maximum.

Characteristic	Northwestern intermountain USA	Southeastern Australia	Northwestern Mediterranean
Climate	Cold-temperate	Warm-temperate	Mediterranean
Mean min–max annual temperature (°C)	0.1–15.3	7.6–20.8	8.8–25.5
Mean annual precipitation (mm)	950	817	650
Peak flow	Early spring	Extreme winter	Usually in winter
Peak leaf fall	Autumn	Summer, dominated by bark, branches, fruit capsules	Summer and autumn
Catchment use	Forestry	Mainly forestry with some tussock grasslands	Forestry and agriculture until 1956
Catchment vegetation	<i>Pseudotsuga menziesii</i> , <i>Pinus ponderosa</i> , <i>Picea engelmannii</i> , <i>Artemisia tridentata</i>	<i>Eucalyptus</i> spp.	<i>Pinus halepensis</i> , <i>Quercus ilex</i>
Riparian vegetation	<i>Alnus incana</i> , <i>Cornus sericea</i> , <i>Acer glabrum</i> , <i>Salix</i> , <i>Betula occidentalis</i>	<i>Eucalyptus</i> spp., <i>Casuarina</i> , <i>Leptospermum</i> , <i>Melaleuca</i> , <i>Pomaderris aspera</i>	<i>Corylus avellana</i> , <i>Cornus sanguinea</i> , <i>Populus nigra</i> , <i>Populus alba</i> , and <i>Rubus ulmifolius</i>
Common disturbances	Peak runoff in spring	Floods, droughts	Floods, seasonal droughts
Other less predictive disturbances	Fire	Long-term drought >10 y, fire	Fire
Date of the fire for this study	19 August–9 September 2007	11 January 2007	10 August 2003
Sampling date	31 July–1 August 2008	8–9 October 2007	14 May–30 July 2004
Macroinvertebrate sampling procedure	Surber net (929 cm ²) samples	4-min multihabitat kick samples	4-min multihabitat kick samples

conditions of the previous months combined with wind to produce an extensive crown fire (Paricio 2007). In 4 days, this fire burned a total forested area of 4543 ha, which included most of the study area.

All 3 biogeographical regions included in our study were similar in that the fires were extensive (affecting most of the burned catchments; see Table 2) and they followed a series of drier-than-average years. We sampled the streams in these biogeographic regions within a similar time frame (9–11 mo) after fire to assess the responses to catchment wildfire of stream macroinvertebrate communities.

Sampling design and sample collection

We sampled a total of 18 streams, 6 streams in each biogeographic region, half of which had burned catchments and half of which were in unburned (control) catchments (Fig. 1, Table 2). Burned and control catchments were near each other, and the streams were physically similar and of a comparable size to minimize abiotic differences other than the effects of fire. We sampled 9–11 mo after fire in each study area along a 50-m reach on each stream that was judged visually to be representative of the

general habitat conditions for that stream. We measured water temperature (°C) and electrical conductivity (μS/cm) with multiparameter probes (model 30 [Yellow Springs Instruments, Yellow Springs, Ohio] in IDA; model U-22 [Horiba Instruments, Irvine, California] in VIC; Multi-line P4 [WTW, Multiline, Weilheim, Germany] in CAT). We estimated discharge (L/s) from mean depth, transect width, and water velocity measurements recorded with flow meters (Model 2000 Flo-Mate [Marsh–McBirney, Frederick, Maryland] in IDA and VIC; miniAir20 flow meter [Schiltknecht, Gossau, Switzerland] in CAT). We visually estimated canopy cover as a percentage of the stream channel shaded by vegetation (Smith and Kraft 2005). To assess the in-stream habitat heterogeneity, physical habitat diversity, and food sources at the stream site, we used the Index of Fluvial Habitability (IHF, with values ranging from 20 to 100; Pardo et al. 2002).

Sampling followed IHF protocols, the common sampling protocols in wilderness stream ecosystems (Davis et al. 2001), and protocols used in biomonitoring. We collected 3 to 5 Surber net samples (250-μm mesh, 929 cm²) in IDA. In VIC and CAT, we collected 3 multihabitat kick samples (250-μm-mesh sweep net) each taken during a

Table 2. Main characteristics and in situ measures of streams in burned (B) and unburned (U) catchments.

Biogeographic region	Status	Stream	Location (Latitude, longitude)	Area (km ²)	Elevation (m asl)	Discharge (L/s)	Specific discharge (L s ⁻¹ km ⁻²)	Catchment burned (%)	Temperature (°C)	Conductivity (μS/cm)	Orientation
Idaho	U	Blackmare	44°48'43"N, 115°45'21"W	4.9	1689	690	141.7	10	10.7	38	E
	U	Camp	44°53'23"N, 115°42'14"W	28.7	1256	53	1.8	10	11.1	68	W
	U	Buckhorn	44°54'44"N, 115°45'10"W	48.8	1228	1276	26.2	10	15.5	38	E
	B	Goat	44°45'20"N, 115°41'04"W	17.2	1472	272	15.8	75	14.1	51	W
	B	Phoebe	44°54'15"N, 115°42'34"W	17.4	1256	48	2.8	85	12.7	86	E
	B	Dollar	44°42'41"N, 115°42'38"W	24.7	1548	349	14.1	80	9.2	40	E
Victoria	U	Moonee	36°30'37"S, 145°33'51"E	26.0	420	14	0.5	0	10.7	42	N
	U	Blue range	36°33'40"S, 146°3'27"E	16.7	420	25	1.5	0	13.4	60	W
	U	White gum gully	36°28'20"S, 145°32'55"E	23.5	503	36	1.5	0	11.7	37	NE
	B	Watchbox	36°25'9"S, 146°6'25"E	31.3	400	2	0.1	86.3	17.6	110	N
	B	Holland	36°33'3"S, 146°9'36"E	9.0	380	16	1.8	60.1	11.1	25	W
	B	Fifteen mile	36°28'57"S, 146°9'56"E	60.7	483	215	3.5	96.2	8.1	31	N
Catalonia	U	Mura	46°9'58"N, 41°34'48"E	2.8	540	150	53.7	0	17.7	563	W
	U	Font del Llor	46°8'35"N, 41°49'2"E	0.9	520	1	1	3	19.6	564	E
	U	Castelló	46°6'56"N, 42°10'58"E	2.9	520	1	0.3	0	18.1	647	W
	B	Gallifa	46°9'52"N, 42°30'59"E	2.9	560	13	4.5	84	18.0	690	S
	B	Vall d'Horta	46°8'19"N, 42°1'12"E	7.6	510	17	2.3	66	20.0	619	SE
	B	Ripoll	46°9'43"N, 42°6'30"E	7.5	487	5	0.7	91	24.5	616	S

4-min period. For 2 streams in CAT (Gallifa and Mura), we grouped samples from different sampling dates (14 May–30 July) to reach the required number of samples per stream. Identification of macroinvertebrates was carried out to the level of genus (Leica MZ6 and MZ8 dissecting microscopes [Leica Microsystems (Schweiz) AG, Heerbrugg, Switzerland]), except that Chironomidae were identified to subfamily level and other Diptera and all other small immature stages were identified to family or order level. We counted all macroinvertebrates in the samples. For highly abundant taxa (>200 individuals in $\frac{1}{4}$ of the sample separated using a grid-square), we extrapolated for the rest of the sample.

Macroinvertebrate community measures and data analysis

To compare stream macroinvertebrate communities in burned and unburned catchments, we calculated taxonomic richness and total abundance (individuals/sample) for each stream. We used rarefaction (Hurlbert 1971) and the nonparametric unbiased variant Chao taxa estimator (Chao and Yang 1993) to estimate species richness. The nonparametric unbiased variant (Chao) taxa estimator is based on extrapolation of accumulation curves and the number of unseen taxa and may provide more meaningful comparisons among disturbed communities sampled from different sized areas than other estimates (McCabe and Gotelli 2000). Rarefaction can standardize collections with samples that differ substantially in abundance. The smallest sample (217 in our study) is used with the previous validation that the number of individuals collected exceeded the asymptote on the accumulation curve (Collins and Simberloff 2007). We also used Whittaker plots to compare the relative taxon cumulative abundance between streams in burned and unburned catchments (R package *BiodiversityR*, version 2.4-4; R Project for Statistical Computing, Vienna, Austria; Kindt and Coe 2008).

We $\ln(x)$ -, \sqrt{x} -, or $\arcsin(x)$ -transformed all macroinvertebrate community measures, % *r*-strategist taxa (Chironomidae, Simuliidae, and Baetidae), and % canopy cover to meet normality assumptions. We compared sites in burned and unburned catchments with a 3-level hierarchical nested analysis of variance (ANOVA) (fire, location within fire, and stream within location). We compared simple in-stream habitat (IHF) and stream canopy cover between sites in burned and unburned catchments with a nested ANOVA (fire and location within fire). All statistical analyses were done in R (version 3.1.0; R Project for Statistical Computing, Vienna, Austria).

For each biogeographic region, we used nonmetric multidimensional scaling (NMDS) with Bray–Curtis and Sørensen distance indices to compare macroinvertebrate community composition between sites in burned and unburned catchments. The Bray–Curtis index is a widely used abundance-based measure of similarity between pairs

of samples and is expected to decrease with increasing geographical distance (Anderson et al. 2011). We calculated this distance after the Wisconsin double standardization procedure (i.e., we divided species abundances by their maxima and then standardized sites by totals; Oksanen et al. 2013). We calculated the Sørensen index, which has been used as a flexible measure of β diversity, as the average distance (dissimilarity) from an individual site to the group centroid (Chao et al. 2006). Both indices exclude joint absences, which means that 2 sites are not considered more similar if they both lack certain species (Anderson et al. 2011), and 2-dimensional ordination plots were used for visual inspection of distances. We used the function *adonis* to test the effects of fire, stream nested within fire, and samples nested within stream for each biogeographic region. The significance test of *adonis* is calculated with pseudo-*F* ratios derived from sequential sums of squares from permutations of semimetric and metric distance matrices partitioning among sources of variation or factors (Oksanen et al. 2013). We ran all multivariate macroinvertebrate community analyses with the R package *vegan* (version 2.0-7; Oksanen et al. 2013).

To examine the impact of wildfire on macroinvertebrate community diversity and to depict the different responses among biogeographic regions, we partitioned the γ diversity into independent α and β richness-equivalent number components using the framework proposed by Jost (2006, 2007). We used the R package *vegetarian* (version 1.2; Charney and Record 2009) to calculate the sample averages of the α Shannon entropy index ($H\alpha$) for each biogeographic region and condition (burned and unburned) and converted this value to an equivalent number by taking its exponent ($\alpha = \exp[H\alpha]$; Jost 2007). Within this framework, diversity indices were converted to number equivalents assuming the multiplicative Whittaker's law (i.e., $\gamma = \alpha\beta$). The total number of taxa recorded within one biogeographic region is γ , the mean number of taxa across the samples within the biogeographic region is α , and β is the effective number of taxonomically distinct samples (Jost 2007). We repeated the calculations for each biogeographic region, separating burned and unburned conditions. We used Shannon diversity because it is a standard diversity measure that can be partitioned into independent components when community weights (e.g., number of individuals) are unequal (Jost 2007).

RESULTS

Regardless of the biogeographic region, sites in burned catchments had lower % canopy cover than sites in unburned catchments (burned: $51 \pm 5\%$ [SE] vs unburned: $65 \pm 4\%$; Fire: $F_{1,14} = 4.52$, $p = 0.05$; Fire(location): $F_{2,14} = 0.52$, $p = 0.60$). The sites in unburned catchments in the 3 biogeographic regions had consistently higher values of the IHF than did the sites in burned catchments (burned:

66 ± 3 vs unburned: 76 ± 3; Fire: $F_{1,14} = 5.89$, $p = 0.03$; Fire(location): $F_{2,14} = 1.28$, $p = 0.31$).

All community measures are shown in Table 3, and their comparison via the 3-level hierarchical nested ANOVA is shown in Table 4. The effects of fire were significant for all macroinvertebrate community measures, as were differences within biogeographic regions and within streams (Table 4). Compared with sites in unburned catchments, sites in burned catchments had lower taxon numbers whether measured as taxonomic richness, rarefied, or Chao taxa estimator (Table 3, Fig. 2A–C). The largest differences between sites in burned and unburned catchments were consistently found in the VIC streams (Fig. 2A–C). All taxonomic richness estimates were ≥35% lower for sites in burned than unburned catchments, and for rarefied taxon richness the difference was >50% (Table 3). Sites in burned catchments in IDA and CAT also had fewer taxa than sites in their unburned counterparts, but the differences were not as strong as in VIC and were always <20%.

Sites in burned catchments had higher macroinvertebrate abundances than sites in unburned catchments, and the strongest differences were observed in VIC where sites in burned catchments had 75% higher abundance than sites in unburned catchments. In CAT this difference

was 45%, whereas in IDA it was 15% (Table 3, Fig. 2D). The proportional abundance of the sum of Chironomidae, Simuliidae, and Baetidae families (i.e., *r*-strategist taxa) was higher at sites in burned than in unburned catchments across the 3 biogeographic study regions, with the difference smallest in CAT. Comparing all biogeographic regions and conditions, the proportional abundance of *r*-strategist taxa was highest at CAT sites, regardless of catchment burn status (Table 3).

The cumulative taxon rank plots again showed the clearest separation between sites in burned and unburned catchments for VIC, where only 4 taxa made up 90% of the cumulative relative abundance in sites in burned catchments (Fig. 3A–C). Similarly, sites in burned and unburned catchments in CAT were dominated by 7 and 8 taxa, respectively, whereas in IDA, more taxa (15 and 18 at sites in burned and unburned catchments, respectively) made up 90% of the macroinvertebrate abundance.

When macroinvertebrate community composition was compared using the Bray–Curtis or Sørensen indices, catchment fire appeared to account consistently and significantly for site variability (9–21%, $p < 0.05$), and individual stream (nested within fire) also explained much variation (37–58%). The sum of the tested factors (i.e., fire, stream within

Table 3. Mean (±1 SE) taxonomic richness, rarefied taxa richness ($n = 217$), Chao taxa estimator, total and *r*-strategist taxa abundances for sites in unburned and burned catchments for all biogeographic regions together and each region separately. IDA = Idaho, VIC = Victoria, CAT = Catalonia, %Chir+Sim+Baet = proportion (%) of the abundance of invertebrates from the Chironomidae, Simuliidae, and Baetidae families.

Biogeographic region	Community parameter	Unburned	Burned
IDA + VIC + CAT	Taxonomic richness	37 ± 1	31 ± 1
	Rarefied taxa richness	23 ± 1	16 ± 1
	Chao taxa estimator	44 ± 10	38 ± 12
	Abundance	1983 ± 415	4862 ± 876
	%Chir+Sim+Baet	51.3 ± 3.9	66.4 ± 6.2
IDA	Taxonomic richness	34 ± 1	30 ± 1
	Rarefied taxa richness	26 ± 1	22 ± 1
	Chao taxa estimator	38 ± 2	38 ± 3
	Abundance	702 ± 64	826 ± 144
	%Chir+Sim+Baet	36.5 ± 2.0	50.5 ± 3.6
VIC	Taxonomic richness	40 ± 4	26 ± 1
	Rarefied taxa richness	24 ± 2	11 ± 0
	Chao taxa estimator	51 ± 4	29 ± 2
	Abundance	1548 ± 214	6174 ± 541
	%Chir+Sim+Baet	55.7 ± 6.1	77.4 ± 7.2
CAT	Taxonomic richness	38 ± 6	37 ± 3
	Rarefied taxa richness	15 ± 1	12 ± 1
	Chao taxa estimator	50 ± 6	47 ± 4
	Abundance	5411 ± 1047	9946 ± 1936
	%Chir+Sim+Baet	76.1 ± 4.6	80.0 ± 5.2

Table 4. Summary of results of the 3-level, hierarchical, nested analysis of variance used to assess the variation of community structure metrics by fire, location (biogeographic region) within fire, and stream within location. Separate analyses were done for all macroinvertebrate community metrics: taxonomic richness, rarefied taxa richness ($n = 217$), Chao taxa estimator, total abundance, and proportion (%) of the abundance of invertebrates from the Chironomidae, Simuliidae, and Baetidae families (%Chir+Sim+Baet). F values are presented with their significance (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, NS = nonsignificant). df = degrees of freedom).

Source	df	Taxonomic richness	Rarefied taxa richness	Chao taxa estimator	Total abundance	%Chir+Sim+Baet
Fire	1	28.16***	104.13***	9.09**	38.89***	38.82***
Fire/location	4	9.39***	57.27***	7.78***	82.37***	63.67***
Fire/location/stream	12	4.92***	4.53***	1.78 ^{NS}	2.26*	7.14***
Residuals	40					

fire, and samples within stream) explained $\geq 67\%$ of the variability and reached 80% in VIC and CAT streams. Visual inspection of the ordination plots revealed similar results for both indices and clearly separated biogeographic regions, and within the regions, a higher faunal overlap between all streams was observed in IDA macroinvertebrate communities (Fig. 4A, B).

The highest equivalent numbers of γ and α diversity were found in IDA followed by VIC and CAT (IDA: $\gamma = 15.56 \pm 0.14$, $\alpha = 10.59 \pm 0.10$; VIC: $\gamma = 11.33 \pm 0.08$, $\alpha = 6.82 \pm 0.04$; CAT: $\gamma = 9.17 \pm 0.04$, $\alpha = 6.04 \pm 0.02$). Both α and β diversity were lower at sites in burned than in unburned catchments. Diversity was least different in IDA streams and most distant in VIC streams (Fig. 5). In con-

trast to the other biogeographic regions, β diversity was higher at sites in burned than in unburned catchments in CAT (Fig. 5).

DISCUSSION

Stream macroinvertebrate community responses

The responses of stream macroinvertebrate communities to catchment wildfire were similar across all biogeographic regions, but the magnitude of these responses varied. In support of our initial expectations, communities at sites in burned catchments showed clear dominance of a few opportunistic taxa, whereas communities at sites in unburned catchments sometimes had more

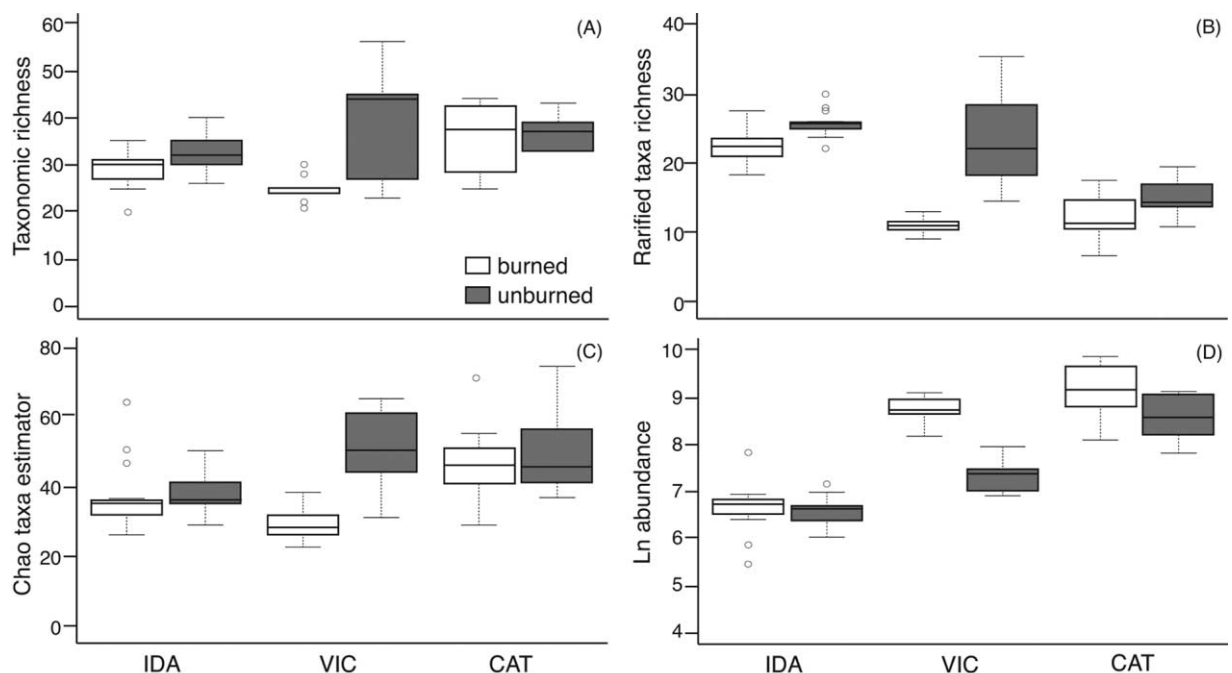


Figure 2. Box-and-whisker plots for taxonomic richness (A), rarefied taxa richness (B), Chao taxa estimator (C), and $\ln(\text{total abundance})$ (D) at sites in burned and unburned catchments in each biogeographic region (IDA = Idaho, VIC = Victoria, CAT = Catalonia). Lines in boxes are medians, box ends are quartiles, whiskers are data extremes that do not exceed $1.5 \times$ the quartile, and data that surpass this limit are plotted as dots.

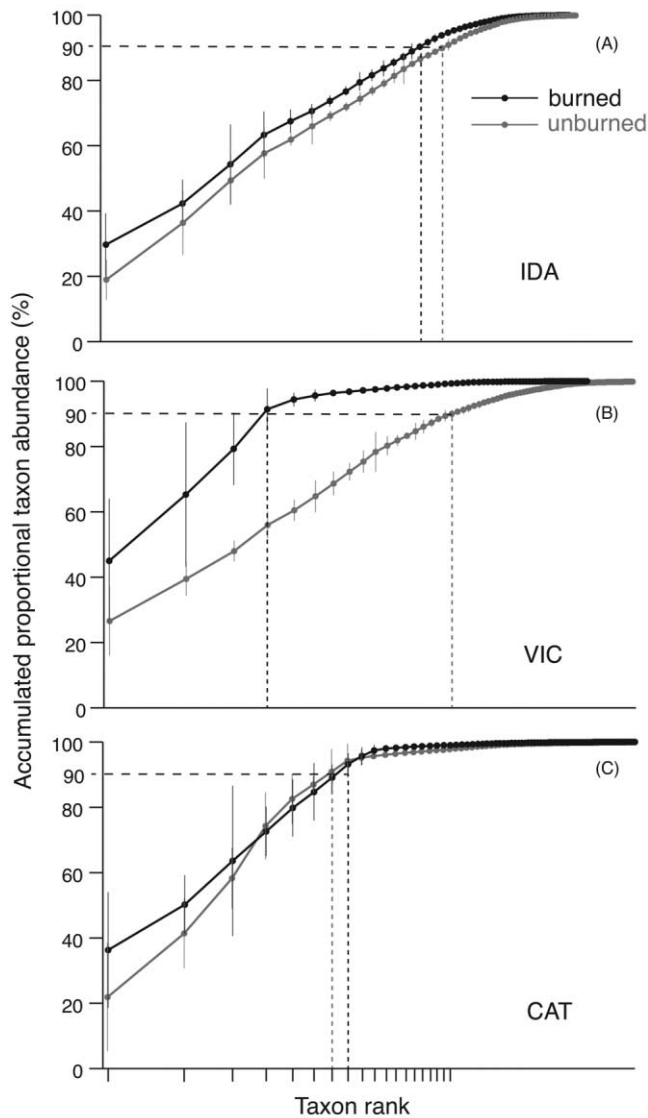


Figure 3. Accumulated proportional taxon abundance (\pm CI) for macroinvertebrate communities in Idaho (IDA) (A), Victoria (VIC) (B), Catalonia (CAT) (C). The dashed lines represent 90% of the accumulated abundance and their respective number of taxa for sites in burned and unburned catchments.

taxa (Fig. 6A, B). Differences between sites in burned and unburned catchments were consistently stronger in VIC than in IDA or CAT streams. In all estimates of taxonomic richness, $\geq 35\%$ of the taxa in VIC appeared to have been adversely affected, whereas this value was $\leq 20\%$ in IDA and CAT. Our observations of greater macroinvertebrate abundance at sites in burned than unburned catchments in the 3 regions are consistent with findings reported in other studies (Minshall et al. 2001c, Mellon et al. 2008, Malison and Baxter 2010, Verkaik et al. 2013a), although postfire dominance of a few opportunistic taxa was most apparent in VIC streams. On the other

hand, the highest % *r*-strategist taxa was found in CAT streams.

After a wildfire, the major changes in aquatic habitat may depend on the severity and extent of fire and the intensity and amount of postfire runoff (Gresswell 1999). The indirect effects of fire on aquatic systems depend largely on catchment erosion and the magnitude of post-fire flows, which may mediate the effect on the biota, the amount and quality of consumable resources (e.g., living space and food), and the condition of the habitat (Minshall 2003). Our simple metrics indicated, as expected, that fire diminished % canopy cover and homogenized the fluvial habitat. However, to understand the differences among the responses within the 3 biogeographic regions and support our 3rd expectation, we can only hypothesize based on our findings and what we know of their climates and hydrologies. We think that climate, via its effects on hydrology and riparian vegetation, was responsible for the

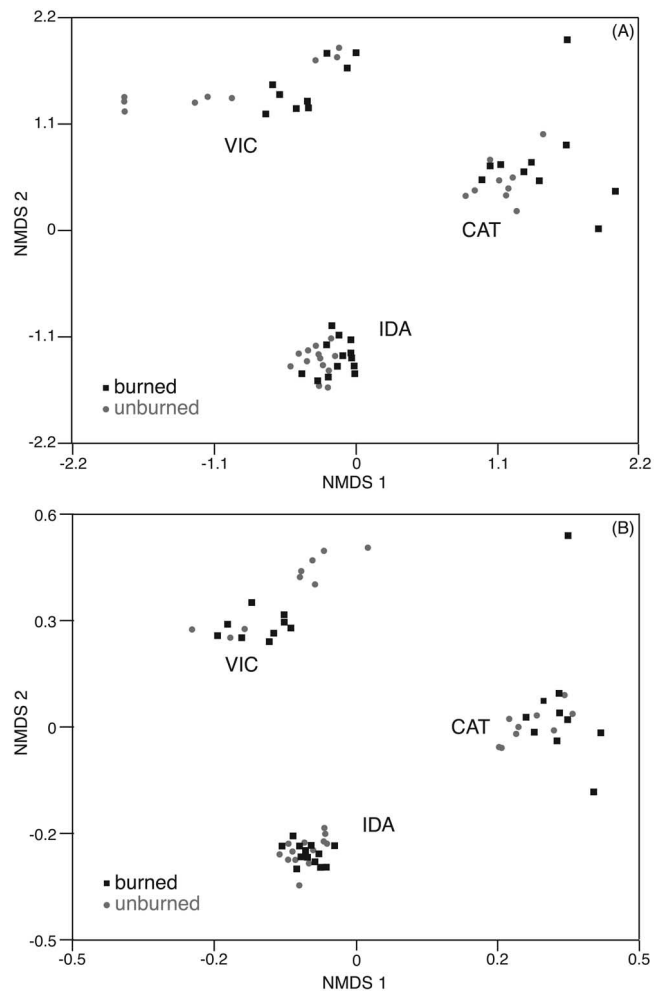


Figure 4. Nonmetric multidimensional scaling ordination plots for all samples based on Bray–Curtis (A) and Sørensen (B) distance for each biogeographic region (IDA = Idaho, VIC = Victoria, CAT = Catalonia).

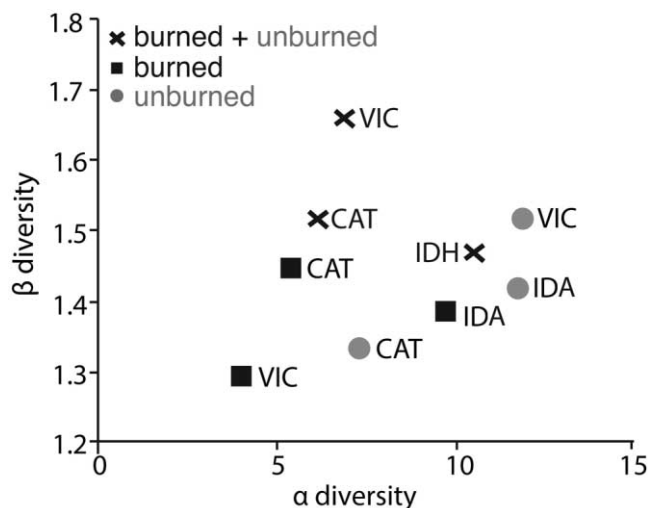


Figure 5. β equivalent number diversity plotted against α equivalent number diversity for all sites (burned and unburned catchments), sites in burned catchments only, and sites in unburned catchments only in Idaho (IDA), Victoria (VIC), and Catalonia (CAT). Error bars were not distinguishable at this scale.

differences because of its influence on: 1) postfire flows and seasonal patterns of hydrology and 2) recovery of the catchment vegetation after the disturbance, which both indirectly affect 3) changes in the input dynamics and storage of allochthonous organic matter.

Streams in Mediterranean regions are characterized by high interannual hydrological seasonality (e.g., in flood intensity, frequency, and flow intermittency; Gasith and Resh 1999). After the dry summer, autumn is generally characterized by heavy rainfall, as occurred in CAT shortly after the fire we studied (Vila-Escalé 2008, Verkaik et al. 2013b). As a consequence of a denuded catchment and reduced water retention and infiltration (Shakesby 2011), sites in burned catchments in this region may have experienced increased runoff and sediment yield into streams. This supposition was corroborated by Vila-Escalé (2008) in CAT, who reported that the in-stream habitat of a stream in a burned catchment changed dramatically, and sediment transport and deposition yield peaked 2 to 8 wk after this fire. In the same study, pre- and postfire macroinvertebrate family richness were similar 309 d after fire, although the macroinvertebrate families composing the community differed (Vila-Escalé 2008), a result consistent with the higher β diversity found in streams in burned catchments. In addition, the dominance of *r*-strategist taxa at CAT streams probably reflects repeated shifting from dry to wet years in these Mediterranean streams (Bêche and Resh 2007). Compared with temperate streams, Mediterranean streams have more macroinvertebrates with small size, active aerial dispersal, strong swimming ability, or aerial respiration (Bonada et al. 2007), which together may facilitate rapid recovery after disturbances.

Flow intermittency characterizes stream hydrology in the VIC streams, and intermittency probably mediated the stream macroinvertebrate responses to fire. Wildfire-related sediment slugs have been recorded between the 1st and 3rd postfire years in alpine Australian streams (Lyon and O'Connor 2008). Based upon visual inspections (described in Verkaik et al. 2014), no large, postfire floods or major changes in stream habitat appeared to have occurred prior to our sampling of the VIC streams. During the drought, rainfall was not strongly correlated with streamflow and this relationship weakened even further as the drought persisted (Verkaik et al. 2014). Thus, drought, habitat fragmentation, and reduction in connectivity may have served as barriers to dispersal for macroinvertebrates (Robson et al. 2011). Compared to the apparent responses to fire in the other regions, recovery of macroinvertebrates in VIC streams in burned catchments may have been impaired by the postfire persistence of low flows associated with continuing severe drought (Thomson et al. 2012), which may have limited the resilience and resistance of the macroinvertebrate assemblages (Peat et al. 2005, Dewson et al. 2007, Robson et al. 2011).

The peak discharge in cold, temperate streams in Idaho typically is associated with spring snowmelt, and its timing and magnitude may influence responses of stream macroinvertebrates to wildfire. In general, snowmelt and associated runoff are fairly predictable phenomena in this region. For instance, a study conducted over 6 summers (1990–1995) in wilderness streams of central Idaho (near those we studied) showed little environmental change as measured by coefficients of variation for substrate size and embeddedness, channel width and depth, and periphyton standing crop (Robinson et al. 2000). In the same study, macroinvertebrate abundance showed low interannual variability, perhaps because of the relatively predictable snowmelt, peak flows, and related disturbances. Streams in burned catchments in IDA probably experience larger-than-usual snowmelt runoff or intense mid-summer rainstorms that may alter channel cross-sections and trigger increases in sediment transport and deposition (Minshall 2003). Such events may or may not occur in, or be most severe in, the 1st year following a fire, and this occurrence may mediate the overall effects of fire on stream macroinvertebrates. For example, after the 1988 Yellowstone wildfires, the peak in sediment load in several streams in burned catchments occurred within a window of 3 or 4 y, and was associated with intense summer rainfall over bare slopes rather than spring runoff (Minshall et al. 1997). This loading caused dramatic changes in stream channel structure and macroinvertebrate communities in the years after fire (see summary in Romme et al. 2011). In our study, visual inspection showed that no major physical geomorphological alterations had occurred since the fire, which may explain why differences between streams in burned and unburned catchments in this region were less pronounced than in the other regions.

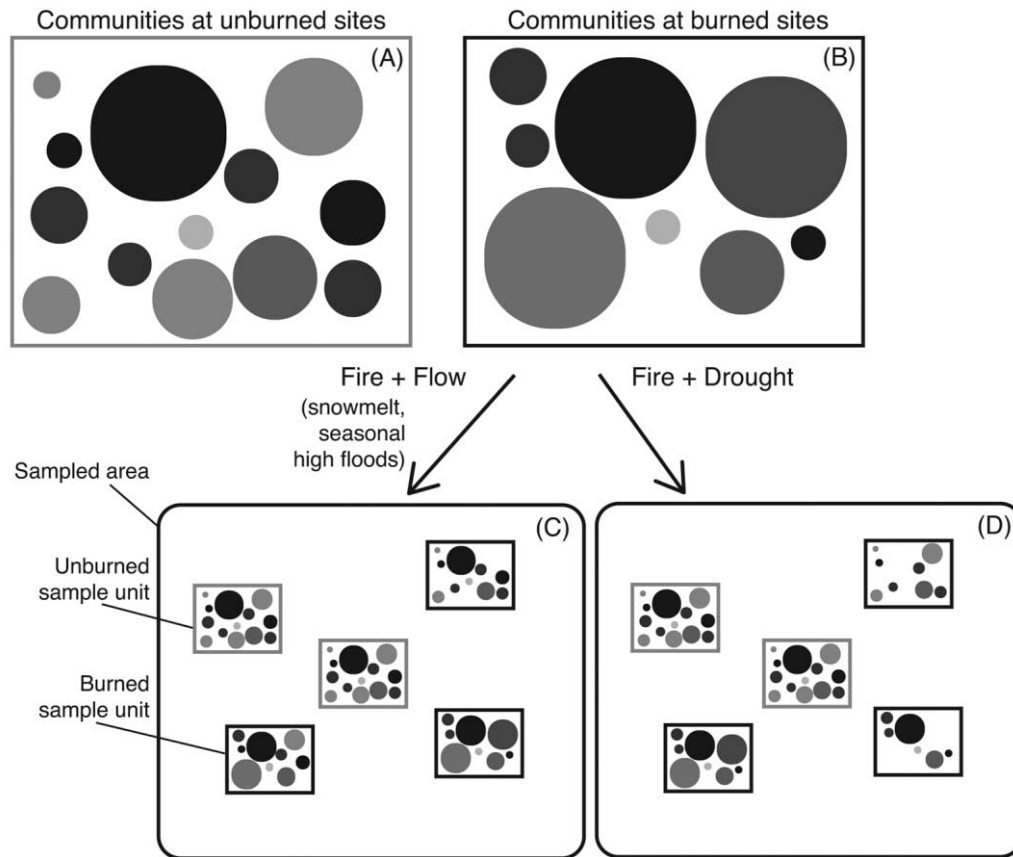


Figure 6. Diagram of the responses of macroinvertebrate communities to catchment fire and potential interactive postfire disturbances. A.—Communities at sites in unburned catchments. B.—Communities at sites in burned catchments. C.—Possible outcomes in communities affected by fire and flow. D.—Possible outcomes in communities affected by fire and drought. Communities at sites in burned catchments (black borders) showed a clear dominance of a few opportunistic taxa (larger circles), whereas communities at sites in unburned catchments (gray borders) sometimes had greater taxon richness (more circles and more shades of grey). Communities at sites in burned and unburned catchments were more similar when predictable postfire disturbances occurred (C) than when disturbed by fire and drought (D) because habitat fragmentation and reduction in connectivity caused by drought may have served as barriers to dispersal for some macroinvertebrates.

In Fig. 6, we illustrate and summarize our interpretation of the variation in stream macroinvertebrate responses to fire and other disturbances. Macroinvertebrate communities disturbed by fire and flows (Fig. 6C), i.e., high seasonal stream flows and flooding in CAT or peak snowmelt runoff in IDA showed lower variation than respective communities at sites in unburned catchments. Thus, predictable postfire disturbances may have overwhelmed the effects of fire, and communities at sites in burned and unburned catchments showed higher similarities in IDA or CAT than in VIC (Fig. 6C). In contrast, macroinvertebrate communities disturbed by fire and enduring drought (Fig. 6D), i.e., in VIC, showed the highest variation among communities in burned catchments and the largest differences between sites in burned and unburned catchments (Fig. 6D), possibly because the combination of fire and low flows created deleterious conditions for some taxa. In addition, the habitat fragmentation and reduction in connectivity caused

by drought may have been barriers to dispersal for some macroinvertebrates.

Longer-term effects of wildfire on stream macroinvertebrate communities

The comparisons in our study were focused on a relatively short period of time after wildfire (<1 y). However, based upon our observations and the published literature, we can speculate on the longer-term effects of wildfire on stream macroinvertebrates in these biogeographic regions. Not all Mediterranean vegetation responds positively after fire (Rodrigo et al. 2004), but these terrestrial ecosystems are commonly considered resilient to fire (Pausas et al. 2008). Under the circumstances of rapid recovery of the vegetation in burned catchments, peak erosion occurs after fires and returns progressively to prefire erosion rates over time (Mayor et al. 2007). In general, the largest changes

occur after the first postfire rains, although vegetation, soil type, topography, fire severity, and extent could all affect the magnitude of changes in geomorphology and substrata (Shakesby 2011). Therefore, the differences in recovery trajectories in Mediterranean streams probably are related to the magnitude, frequency, and timing of heavy rains (Verkaik et al. 2013a). Thus, although indirect fire effects may result in a press response, macroinvertebrates in streams draining burned Mediterranean catchments may be restructured by subsequent pulse disturbances of high flows, especially by the first big flow occurring postfire. Interannual differences in hydrology also could interact to influence macroinvertebrate resilience, and drought (seasonal or interannual) may play an overriding role in these streams (Vila-Escalé 2008, Verkaik et al. 2013b).

Compared with the native coniferous vegetation of Mediterranean forests, the postfire recovery of eucalypt vegetation in southeast Australia can be quite rapid (Shakesby et al. 2007). After fire, eucalypt forest vegetation may produce a rapid build-up of leaf cover through regrowth from epicormic buds and lignotuber shoots. This regrowth may provide shade and a supply of allochthonous resources to streams in burned catchments. Moreover, this relatively rapid recovery of catchment vegetation may simultaneously lessen the potential fire effects of erosion (Nyman et al. 2011). However, if drought occurs simultaneously with fire, it may impair recovery of macroinvertebrate communities. In this sense, macroinvertebrates in streams in burned catchments in VIC appear to have been subjected to a ramp disturbance, largely constrained by drought. During drought, the local extinction of stream macroinvertebrates could depend on their resistance to the loss of flow and surface water although other factors, such as the initial species pool and the extent of human disturbance of a catchment, are likely to be important (Boulton and Lake 2008). The longer-term consequences of drought are less predictable, and responses of macroinvertebrates to the reestablishment of flows can be highly variable (Lake 2011). Shortly after our study, a La Niña event peaked in late 2010 and 2011 in eastern Australia and gave rise to widespread flooding between September 2010 and February 2011 (Van den Honert and McAneney 2011). These floods no doubt affected the study site, but the consequences and responses are unknown.

In temperate ecosystems like Idaho, recovery of coniferous forests and riparian shrubs after fire appears to be slower, though highly variable, than in Mediterranean and eucalypt forests. Allochthonous inputs may be reduced in some cases (e.g., Jackson et al. 2012), but roots of riparian shrubs generally survive and resprout in the 1st postfire year, which subsequently may result in higher litter input in other years (Romme et al. 2011). Increases in channel erosion and organic matter may occur after catchment fire, but can take place any time within a broad window of several years after fire (Minshall et al. 1997, Romme et al.

2011, Rugenski and Minshall 2014). Postfire streams in this region may exhibit greater year-to-year variation in sediment loads, organic debris, large woody debris, and undercut bank structure rather than a simple perennial increase in scour (Arkle et al. 2010). Furthermore, debris flows in this region (liquefied landslides often triggered by winter rain-on-snow or severe summer thunderstorms) may follow wildfire, and whether these occur or not may strongly mediate the consequences of fire for stream ecosystems (Cover et al. 2010, Harris et al. 2015). Thus, compared with the other biogeographic regions, responses to fires in catchments of streams in Idaho may be equivalent to a press effect. In any case, climate change may be altering the magnitude and predictability of spring high flows in this region (Davis et al. 2013b), and, in turn, this effect may mean changes in the nature of responses by stream ecosystems to fire (Davis et al. 2013a, Rugenski and Minshall 2014). Longer-term studies have shown that reduction in the magnitude of spring runoff (resulting from a lower than normal snowpack) may ameliorate the effects of catchment fire in these streams (Rugenski and Minshall 2014), but moderation may depend on the trajectory of riparian vegetation recovery (CVB and GWM, unpublished data). Furthermore, in at least some areas of the Idaho region, the trajectory of postfire recovery of vegetation is uncertain in the context of changing climate. For example, rather than a return to prefire forested conditions, some regions may undergo a postfire transition toward a shrub–steppe state, with unknown consequences for stream ecosystems (Davis et al. 2013a).

Conclusions

Fires can cause dramatic changes in the structure and function of terrestrial and aquatic ecosystems (Romme et al. 2011). Effects of fire on aquatic systems may depend on fire attributes and may be direct and immediate or indirect and sustained over an extended period (Gresswell 1999). Moreover, the magnitude of stream macroinvertebrate community responses several months after fire can vary depending upon the occurrence of other, potentially interactive, disturbances. Fire, either combined with high flows or drought, was associated with reduced measures of macroinvertebrate community diversity and an increase in abundance, especially of *r*-strategist taxa. Our findings suggest that flows (snowmelt, seasonal high flows) may reestablish or reset the recolonization process, but drought may lessen the resilience and resistance of the macroinvertebrate communities.

Fires, floods, and droughts can create both spatial and temporal heterogeneity and can serve as environmental filters to eliminate or reduce some biota and create opportunities for others. Our findings suggest that these disturbances act as strong filters that shape macroinvertebrate communities in streams among and within regions and

corroborate the ecological importance of disturbance in streams (Resh et al. 1988, Fisher and Grimm 1991, Lake 2000, Stanley et al. 2010). Macroinvertebrate community resilience may be overwhelmed by more prolonged and severe disturbances (Rose et al. 2008). Public perception of fire and fire management have continued to evolve in the last decade (Romme et al. 2011, Moritz et al. 2014), and it may be important to consider drought-management measures that engender resilience in the future (Lake 2011). Separating the effects of drought from wildfire is generally difficult, and, in the context of changing climate, they are likely to occur together more often in the future. Long-term studies of the effects of large-scale disturbances like wildfire on lotic macroinvertebrate communities are rare (Minshall et al. 1997, Turner et al. 2003, Romme et al. 2011, Ruginski and Minshall 2014). However, these types of investigations are necessary to understand and better predict the responses of stream ecosystems to climate change and shifts in disturbance regimes caused by events such as wildfire, floods, and drought.

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LITERATURE CITED

- Anderson, M. J., T. O. Crist, J. M. Chase, M. Vellend, B. D. Inouye, A. L. Freestone, N. J. Sanders, H. C. Howard, L. S. Comita, K. F. Davies, S. P. Harrison, N. J. B. Kraft, J. C. Stegen, and N. G. Swenson. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters* 14:19–28.
- Arkle, R. S., P. S. Pilliod, and K. Strickler. 2010. Fire, flow and dynamic equilibrium in stream macroinvertebrate communities. *Freshwater Biology* 55:299–314.
- Bêche, L. A., and V. H. Resh. 2007. Short-term climatic trends affect the temporal variability of macroinvertebrates in California “Mediterranean” streams. *Freshwater Biology* 52:2317–2339.
- Bender, E., T. Case, and M. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1–13.
- Betts, E. F., and J. B. Jones. 2009. Impact of wildfire on stream nutrient chemistry and ecosystem metabolism in boreal forest catchments of interior Alaska. Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado. (Available from: Institute of Arctic and Alpine Research UCB 450, University of Colorado, Boulder, Colorado 80309-0450 USA.)
- Bonada, N., S. Dolédec, and B. Statzner. 2007. Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: implications for future climatic scenarios. *Global Change Biology* 13:1658–1671.
- Bond, N. R., P. S. Lake, and A. H. Arthington. 2008. The impacts of drought on freshwater ecosystems: an Australian perspective. *Global Change Biology* 13:1658–1671.
- Boulton, A. J., and P. S. Lake. 2008. Effects of drought on stream insects and its ecological consequences. Pages 81–102 *in* J. Lancaster and R. A. Briers (editors). *Aquatic insects: challenges to populations*. Proceedings of the Royal Entomological Society’s 24th Symposium. Royal Entomological Society, Trowbridge, UK.
- Chao, A., R. L. Chazdon, R. K. Colwell, and T. J. Shen. 2006. Abundance-based similarity indices and their estimation when there are unseen species in samples. *Biometrics* 62:361–371.
- Chao, A., and M. C. K. Yang. 1993. Stopping rules and estimation for recapture debugging with unequal failure rates. *Biometrika* 80:193–201.
- Charney, N., and S. Record. 2009. *Vegetarian: Jost diversity measures for community data*. R Project for Statistical Computing, Vienna, Austria.
- Clarke, A., R. Mac Nally, N. R. Bond, and P. S. Lake. 2010. Conserving macroinvertebrate diversity in headwater streams: the importance of knowing the relative contributions of α and β diversity. *Diversity and Distributions* 16:725–736.
- Collins, M. D., and D. Simberloff. 2007. Rarefaction and non-random spatial dispersion patterns. *Environmental and Ecological Statistics* 16:89–103.
- Cover, M. R., J. A. de la Fuente, and V. H. Resh. 2010. Catastrophic disturbances in headwater streams: the long-term ecological effects of debris flows and debris floods in the Klamath Mountains, northern California. *Canadian Journal of Fisheries and Aquatic Sciences* 67:1596–1610.
- Cowell, A. L., T. G. Matthews, and P. R. Lind. 2006. Effect of fire on benthic algal assemblage structure and recolonization in intermittent streams. *Austral Ecology* 31:696–707.
- Davis, J. C., G. W. Minshall, C. T. Robinson, and P. Landres. 2001. *Monitoring wilderness stream ecosystems*. Rocky Mountain Research Station, USDA Forest Service General Technical Report RMRS-GTR-70. US Department of Agriculture Forest Service, Ogden, Utah.
- Davis, J. M., C. V. Baxter, and G. W. Minshall. 2013a. Climate induced shift in hydrological regime alters basal resource dynamics in a wilderness river ecosystem. *Freshwater Biology* 58:306–319.
- Davis, J. M., C. V. Baxter, E. J. Rosi-Marshall, J. L. Pierce, and B. T. Crosby. 2013b. Anticipating stream ecosystem responses to climate change: toward predictions that incorporate effects via land–water linkages. *Ecosystems* 16:909–922.
- Dewson, Z. S., A. B. W. James, and R. G. Death. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* 26:401–415.
- Dodds, W. K. 2002. *Freshwater ecology. Concepts and environmental applications*. 1st edition. Academic Press, San Diego, California.
- Downes, B. J., P. S. Lake, A. Glaister, and J. A. Webb. 1998. Scales and frequencies of disturbances: rock size, bed pack-

- ing and variation among upland streams. *Freshwater Biology* 40:625–639.
- Fisher, S. G., and N. B. Grimm. 1991. Pages 196–221 in J. Cole, G. Lovett, and S. Findlay (editors). *Streams and disturbance: are cross-ecosystem comparisons useful? Comparative analyses of ecosystems*. Springer-Verlag, New York.
- Gasith, A., and V. H. Resh. 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics* 30:51–81.
- Glasby, T. M., and A. J. Underwood. 1996. Sampling to differentiate between pulse and press perturbations. *Environmental Monitoring and Assessment* 42:241–252.
- Graham, R., T. B. Jain, and M. Loseke. 2009. Fuel treatments, fire suppression, and their interactions with wildfire and its effects: the Warm Lake experience during the Cascade complex of wildfires in central Idaho. USDA Forest Service General Technical Report RMRS-GTR-229. Rocky Mountain Research Station, US Department of Agriculture Forest Service, Fort Collins, Colorado.
- Gresswell, R. E. 1999. Fire and aquatic ecosystems in forested biomes of North America. *Transactions of the American Fisheries Society* 128:193–221.
- Harris, H., C. V. Baxter, and J. M. Davis. 2015. Debris flows amplify effects of wildfire on magnitude and composition of tributary subsidies to main-stem habitats. *Freshwater Science* 34:1457–1467.
- Heyerdahl, E. K., P. Morgan, and J. P. Riser. 2008. Multi-season climate synchronized historical fires in dry forests (1650–1900), northern Rockies, U.S.A. *Ecology* 89:705–16.
- Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology* 52:577–586.
- Jackson, B. K., S. M. P. Sullivan, and R. L. Malison. 2012. Wildfire severity mediates fluxes of plant material and terrestrial invertebrates to mountain streams. *Forest Ecology and Management* 278:27–34.
- Jost, L. 2006. Entropy and diversity. *Oikos* 113:363–375.
- Jost, L. 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439.
- Kindt, R., and R. Coe. 2008. BiodiversityR: GUI for biodiversity and community ecology analysis. R Project for Statistical Computing, Vienna, Austria.
- Krawchuk, M. A., M. A. Moritz, M. A. Parisien, J. Van Dorn, and K. Hayhoe. 2009. Global pyrogeography: the current and future distribution of wildfire. *PloS ONE* 4:e5102.
- Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19:573–592.
- Lake, P. S. 2011. *Drought and aquatic ecosystems: effects and responses*. Wiley-Blackwell, Chichester, UK.
- Lavorel, S., M. D. Flannigan, E. F. Lambin, and M. C. Scholes. 2007. Vulnerability of land systems to fire: interactions among humans, climate, the atmosphere, and ecosystems. *Mitigation and Adaptation Strategies for Global Change* 12:33–53.
- Lepori, F., and N. Hjerdt. 2006. Disturbance and aquatic biodiversity: reconciling contrasting views. *BioScience* 56:809–818.
- Lyon, J. P., and J. P. O'Connor. 2008. Smoke on the water: can riverine fish populations recover following a catastrophic fire-related sediment slug? *Austral Ecology* 33:794–806.
- Lytle, D. A. 2008. Life-history and behavioural adaptations to flow regime in aquatic insects. Pages 122–138 in J. Lancaster and R. A. Briers (editors). *Aquatic insects: challenges to populations*. Proceedings of the Royal Entomological Society's 24th Symposium. Royal Entomological Society, Trowbridge, UK.
- Mackay, R. J. 1992. Colonization by lotic macroinvertebrates: a review of processes and patterns. *Canadian Journal of Fisheries and Aquatic Sciences* 49:617–628.
- Malison, R. L., and C. V. Baxter. 2010. The fire pulse: wildfire stimulates flux of aquatic prey to terrestrial habitats driving increases in riparian consumers. *Canadian Journal of Fisheries and Aquatic Sciences* 67:570–579.
- Malmqvist, B., and S. Rundle. 2002. Threats to the running water ecosystems of the world. *Environmental Conservation* 29:134–153.
- Mayor, A. G., S. Bautista, J. Llovet, and J. Bellot. 2007. Post-fire hydrological and erosional responses of a Mediterranean landscape: seven years of catchment-scale dynamics. *Catena* 71:68–75.
- McCabe, D. J., and N. J. Gotelli. 2000. Effects of disturbance frequency, intensity, and area on assemblages of stream macroinvertebrates. *Oecologia* (Berlin) 124:270–279.
- Mellon, C. D., M. S. Wipfli, and J. L. Li. 2008. Effects of forest fire on headwater stream macroinvertebrate communities in eastern Washington, U.S.A. *Freshwater Biology* 53:2331–2343.
- Mihuc, T. B., and G. W. Minshall. 1995. Trophic generalists vs. trophic specialists: implications for food web dynamics in post-fire streams. *Ecology* 76:2361–2372.
- Minshall, G. W. 2003. Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management* 178:155–161.
- Minshall, G. W., J. T. Brock, D. A. Andrews, and C. T. Robinson. 2001a. Water quality, substratum and biotic responses of five central Idaho (USA) streams during the first year following the Mortar Creek fire. *International Journal of Wildland Fire* 10:185–199.
- Minshall, G. W., C. T. Robinson, and D. E. Lawrence. 1997. Postfire responses of lotic ecosystems in Yellowstone National Park, U.S.A. *Ecology* 54:2509–2525.
- Minshall, G. W., C. T. Robinson, D. E. Lawrence, D. A. Andrews, and J. T. Brock. 2001b. Benthic macroinvertebrate assemblages in five central Idaho (USA) streams over a 10-year period following disturbance by wildfire. *International Journal of Wildland Fire* 10:201–213.
- Minshall, G. W., T. V. Royer, and C. T. Robinson. 2001c. Response of the Cache Creek macroinvertebrates during the first 10 years following disturbance by the 1988 Yellowstone wildfires. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1077–1088.
- Moritz, M. A., E. Batllori, R. A. Bradstock, A. M. Gill, J. Handmer, P. F. Hessburg, J. Leonard, S. McCaffrey, D. C. Odion, T. Schoennagel, and A. D. Syphard. 2014. Learning to coexist with wildfire. *Nature* 515:58–66.
- Nyman, P., G. J. Sheridan, H. G. Smith, and P. N. J. Lane. 2011. Evidence of debris flow occurrence after wildfire in upland catchments of south-east Australia. *Geomorphology* 125:383–401.
- Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens, and H. Wagner. 2013. *Vegan: community ecology package*. R Project for Statistical Computing, Vienna, Austria.

- Pardo, I., S. Vivas, J. Alba-Tercedor, S. Robles, and M. Toro. 2002. El hábitat de los ríos mediterráneos. Diseño de un índice de diversidad de hábitat. *Limnética* 21:115–133.
- Paricio, S. 2007. Comparació d'un sòl cremat i d'un de no cremat de l'incendi de Sant Llorenç de Munt i l'Obac de l'agost del 2003. Pages 253–259 in J. Hernandez, J. Melero, and J. Grau (editors). VI Trobada d'Estudiosos de Sant Llorenç de Munt i l'Obac. Deputació de Barcelona, Barcelona, Spain.
- Pausas, J. G., J. Llovet, A. Rodrigo, and R. Vallejo. 2008. Are wildfires a disaster in the Mediterranean basin? – A review. *International Journal of Wildland Fire* 17:713–723.
- Peat, M., H. Chester, and R. Norris. 2005. River ecosystem response to bushfire disturbance: interaction with flow regulation. *Australian Forestry* 68:153–161.
- Poff, N. L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society* 11:86–92.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, B. Wallace, and R. C. Wissmar. 1988. The role of disturbance in stream ecology. *Journal of the North American Benthological Society* 7:433–455.
- Robinson, C. T., G. W. Minshall, and T. V. Royer. 2000. Interannual patterns in macroinvertebrate communities of wilderness streams in Idaho, USA. *Hydrobiologia* 421:187–198.
- Robson, B. J., E. T. Chester, and C. M. Austin. 2011. Why life history information matters: drought refuges and macroinvertebrate persistence in non-perennial streams subject to a drier climate. *Marine and Freshwater Research* 62:801–810.
- Roby, K. B., and D. L. Azuma. 1995. Changes in a reach of a northern California stream following wildfire. *Environmental Management* 19:591–600.
- Rodrigo, A., J. Retana, and X. Picó. 2004. Direct regeneration is not the only response of Mediterranean forests to large fires. *Ecology* 85:716–729.
- Romme, W. H., M. S. Boyce, R. E. Gresswell, E. H. Merrill, G. W. Minshall, C. Whitlock, and M. G. Turner. 2011. Twenty years after the 1988 Yellowstone fires: lessons about disturbance and ecosystems. *Ecosystems* 14:1196–1215.
- Rose, P., L. Metzeling, and S. Catzirikis. 2008. Can macroinvertebrate rapid bioassessment methods be used to assess river health during drought in south eastern Australian streams? *Freshwater Biology* 53:2626–2638.
- Rugenski, A. T., and G. W. Minshall. 2014. Climate-moderated responses to wildfire by macroinvertebrates and basal food resources in montane wilderness streams. *Ecosphere* 5:1–24.
- Santos, X., V. Bros, and À. Miño. 2009. Recolonization of a burned Mediterranean area by terrestrial gastropods. *Biodiversity and Conservation* 18:3153–3165.
- Shakesby, R. A. 2011. Post-wildfire soil erosion in the Mediterranean: review and future research directions. *Earth-Science Reviews* 105:71–100.
- Shakesby, R. A., P. J. Wallbrink, and S. H. Doerr. 2007. Distinctiveness of wildfire effects on soil erosion in south-east Australian eucalypt forests assessed in a global context. *Forest Ecology and Management* 238:347–364.
- Smith, R. 2007. Key issues identified from operational reviews of major fires in Victoria 2006/07. Department of Sustainability and Environment, Melbourne, Victoria, Australia. (Available from: http://web.archive.org/web/20091002180147/http://www.cfa.vic.gov.au/documents/major_fire_review_06_07.pdf)
- Smith, T., and C. Kraft. 2005. Stream fish assemblages in relation to landscape position and local habitat variables. *Transactions of the American Fisheries Society* 134:430–440.
- Stanley, E. H., S. M. Powers, and N. R. Lottig. 2010. The evolving legacy of disturbance in stream ecology: concepts, contributions, and coming challenges. *Journal of the North American Benthological Society* 29:67–83.
- Thomson, J. R., N. R. Bond, S. C. Cunningham, L. Metzeling, P. Reich, R. M. Thompson, and R. Mac Nally. 2012. The influences of climatic variation and vegetation on stream biota: lessons from the Big Dry in southeastern Australia. *Global Change Biology* 18:1582–1596.
- Tily, C. 2008. Annual fire report 2007. Payette National Forest. US Department of Agriculture Forest Service, McCall, Idaho. (Available from: http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fsm9_030887.pdf)
- Turner, M. G., S. L. Collins, A. L. Lugo, J. J. Magnuson, T. S. Rupp, and F. J. Swanson. 2003. Disturbance dynamics and ecological response: the contribution of long-term ecological research. *BioScience* 53:46–56.
- Van den Honert, R. C., and J. McAneney. 2011. The 2011 Brisbane Floods: causes, impacts and implications. *Water* 3:1149–1173.
- Verkaik, I., N. Prat, M. Rieradevall, P. Reich, and P. S. Lake. 2014. Effects of bushfire on macroinvertebrate communities in south-east Australian streams affected by a megadrought. *Marine and Freshwater Research* 65:359–369.
- Verkaik, I., M. Rieradevall, S. D. Cooper, J. M. Melack, T. L. Dudley, and N. Prat. 2013a. Fire as a disturbance in Mediterranean climate streams. *Hydrobiologia* 719:353–382.
- Verkaik, I., M. Vila-Escalé, M. Rieradevall, and N. Prat. 2013b. Seasonal drought plays a stronger role than wildfire in shaping macroinvertebrate communities of Mediterranean streams. *International Review of Hydrobiology* 98:271–283.
- Vieira, N., W. Clements, and L. Guevara. 2004. Resistance and resilience of stream insect communities to repeated hydrologic disturbances after a wildfire. *Freshwater Biology* 49:1243–1259.
- Vila-Escalé, M. 2008. Efectes d'un incendi forestal en una riera mediterrània (Sant Llorenç del Munt, 2003). PhD Thesis, Universitat de Barcelona, Barcelona, Spain.